

The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts

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A new specimen from the base of the Beaufort Group, Upper Permian of South Africa, represents a new therapsid ('mammal-like reptile') which has been identified as the most basal ('primitive') member of the Anomodontia. *Anomocephalus africanus* gen. et sp. nov. is based upon a partial skull that exhibits several characteristic anomodont synapomorphies including the presence of isodont marginal teeth and a dorsally bowed zygoma, but is distinguished from other anomodonts by the possession of peg-like marginal dentition with oblique wear facets on the tips of the teeth. *Anomocephalus* is excluded from a clade comprised of all other anomodonts as (i) the snout is relatively long, (ii) the vertically aligned zygomatic process of the squamosal is blade-like, and (iii) the squamosal does not contact the ventral tip of the postorbital. The basal position of *Anomocephalus*, together with its South African occurrence, strongly supports the postulate that a Gondwanan distribution was ancestral for anomodonts.

Keywords: Anomodontia; biogeography; palaeontology; phylogeny; Therapsida

1. INTRODUCTION

The most common and widespread terrestrial vertebrates during Late Permian and Triassic times were therapsids of the clade Anomodontia. The tremendous taxonomic and ecological success of the group has traditionally been attributed to the herbivorous diet that is thought to characterize the most diverse anomodont group, Dicynodontia (Hotton 1986; King 1988). The evolutionary history of the dicynodonts is preserved best in the rocks of the Beaufort Group, South Africa and it is the South African forms in which the phenomenon of herbivory has been examined thoroughly. Dicynodonts possess a number of features that have been related to herbivory, including the presence of tusk-like caniniform teeth and a horny beak, the development of a bony secondary palate and the enlargement of the temporal arcade serving as the origin of enlarged and modified jaw adductor musculature (King 1988, 1990). The stepwise acquisition of these features and, thus, the evolution of herbivory in these therapsids can be traced in a series of phylogenetically successive non-dicynodont or 'basal' anomodonts (King *et al.* 1989; King 1994).

Basal anomodonts have traditionally been placed in either Dromasauria or Venyukovioidea (Watson & Romer 1956). The former group was comprised of the southern African taxa *Galechirus*, *Galepus* and *Galeops*, whereas the latter consisted of the Eastern European taxa *Otsheria* and *Venyukovia* (the latter nomen is commonly misspelt '*Venjukovia*': Ivakhnenko 1994, 1996). Both groups were regarded as monophyletic (Brinkman

1981; Hopson & Barghusen 1986) and this implied independent evolutionary radiations in Gondwana and Euramerica respectively by dromasaurs and venyukovioids. However, the analysis of *Patranomodon*, from the base of the Beaufort Group and then the most basal anomodont known, led Rubidge & Hopson (1990) to conclude that both Dromasauria and Venyukovioidea were paraphyletic. A corollary of their evaluation of basal anomodont relationships suggested that these anomodonts were dispersing freely between Gondwanan and Euramerican portions of Pangea. A reappraisal of the Rubidge & Hopson (1990) analysis concurred that 'Dromasauria' was indeed unnatural, yet reaffirmed the monophyly of Venyukovioidea (Modesto & Rybczynski 1999). The results of the latter study indicated that basal anomodonts were not dispersing as freely as Rubidge & Hopson (1990) had suggested and further suggested that an African (Gondwanan) distribution was ancestral for anomodonts and possibly for all therapsids crownwards of Dinocephalia. That conclusion, however, was contingent on the assumption that the most basal members of Therocephalia and Gorgonopsia, successive outgroups to Anomodontia in the study, were African taxa (Modesto & Rybczynski 1999). Gorgonopsian phylogeny is not well known and the interrelationships of therocephalians remain to be established with any confidence (van den Heever 1994). Should a European taxon of the latter group turn out to be the most basal member of the group, the biogeographic conclusions of Modesto & Rybczynski (1999) for Anomodontia will be thrown into doubt.

Patranomodon is known from a single skeleton retrieved from the *Eodicynodon* Assemblage Zone of the Beaufort

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Group, South Africa (Rubidge & Hopson 1996). This biozone preserves the oldest terrestrial vertebrate fauna known in Gondwana (Rubidge 1995). Recent collecting efforts at the base of the Beaufort Group elsewhere in the Karoo Basin, part of a continuing programme by B. Rubidge to determine the lateral extent of the *Eodicynodon* Assemblage Zone along the Ecca–Beaufort contact, have produced therapsid specimens representing new taxa that are strikingly different from those that have been described from the biozone. Among these is a partial skull, bearing a distinctive dentition, collected from a locality near Williston, Northern Cape Province. The skull clearly represents a new species of basal anomodont. We present here a preliminary description of the new species and evaluate the biogeographic implications of its phylogenetic position among other basal anomodonts.

2. MATERIALS AND METHODS

The specimen, BP/1/5582, is housed in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand and consists of a skull with associated disarticulated post-crania. The bone is preserved in a hard mudrock and, therefore, was prepared mechanically by a scribe. Only the right side of the skull is present and it is exposed in lateral view. The post-crania of BP/1/5582 comprise mainly scrappy bones that may not belong with the skull, bear little information of phylogenetic usefulness and will not be considered further in this paper.

3. SYSTEMATIC PALAEONTOLOGY

Therapsida Broom 1905

Anomodontia Owen 1859

Anomocephalus africanus gen. et sp. nov.

(a) *Diagnosis*

This taxon is a large basal anomodont distinguished from other therapsids by the presence of robust, peg-like marginal teeth with canted wear facets and a reduced count of two premaxillary teeth.

(b) *Holotype*

BP/1/5582 (figure 1) is the right side of a skull missing the frontal, postfrontal and parietal entirely and portions of the squamosal, postorbital and braincase. Several poorly preserved postcranial elements are associated with the skull.

(c) *Horizon and locality*

BP/1/5582 is from the base of the Beaufort Group, Upper Permian, near Williston, Northern Cape Province, Republic of South Africa.

(d) *Etymology*

The generic name is from the Greek words *anomos* and *cephalos*, meaning 'lawless' and 'head', respectively. The former word is taken from the prefix of the nomen Anomodontia, the therapsid clade to which the new species belongs, whereas the latter is a common suffix given to therapsid generic names. The specific epithet *africanus* is from Latin and means 'belonging to Africa'.

4. DESCRIPTION

BP/1/5582 is the largest known skull of a basal anomodont, extending ca. 21 cm from the anterior tip of the premaxilla to the posterior margin of the squamosal. The preorbital region occupies ca. 45% of this length and, thus, is relatively longer than those of other anomodonts. However, it is still conspicuously shorter than those of more basal synapsids such as biarmosuchians and sphenacodontids, where this figure ranges from 62–65%.

The premaxilla is dominated by the deep alveolar portion which has room for two teeth. Only the first tooth remains in its socket; the second appears to lie closely in association. Both expand slightly in diameter towards the tip and feature canted wear surfaces. The organization of the succeeding dentition in the maxilla is hidden by a series of disarticulated marginal teeth, some of which may belong to this bone. The best preserved resemble those of the premaxilla but differ in possessing narrower necks and wear on the tips that is slightly more concave than that on the anterior teeth. The maxilla is relatively elongate for an anomodont, on a par with the relatively long snout. It formed the posterior border of the external naris and, although the dorsal lamina has weathered away, it presumably extended upwards and backwards to border the nasal and the prefrontal and lacrimal, respectively. Details of the sutures with the lacrimal and jugal are obscured slightly by overlying sclerotic elements. Posteriorly, the maxilla bears the characteristic anomodont curvature of the free ventral margin forming the base of the dorsally bowed zygomatic arch. The nasal, prefrontal and lacrimal are present and what is visible of these bones resembles in general form and relations those of other basal anomodonts.

The jugal has a marginally greater exposure on the face than other anomodonts. It tapers posteriorly to a slender, rod-like portion immediately posterior to the postorbital bar and then increases gradually in height and twists slightly as it comes to underlie the anterior process of the squamosal. The postorbital bone is a conspicuously flat, curved element that tapers ventrally and fails to reach the zygomatic arch. Unfortunately, the posterodorsal process, which would have formed the upper margin of the temporal opening, is missing. The squamosal was probably triradiate as in other anomodonts but only the anterior and ventral processes remain. The former is a long triangular blade that falls short of the level of the postorbital bar and, thus, resembles those of more basal therapsids rather than other anomodonts where the squamosal extends beyond the bar and contacts the postorbital bone. The ventral process of the squamosal flares posterolaterally revealing the dorsal lamellae of the quadratojugal and quadrate, which are appressed to its anterolaterally orientated inner surface. A small fragment of basioccipital underlies the posterior margin of the squamosal; little more than the margin of the condyle can be seen.

The dorsal lamella of the quadratojugal is relatively broader anteroposteriorly than that of basal anomodonts and so more closely resembles that of dicynodonts. The ventral foot of the quadratojugal, formerly overlying the lateral condyle of the quadrate, is present but is too poorly preserved for adequate description. Only the dorsal

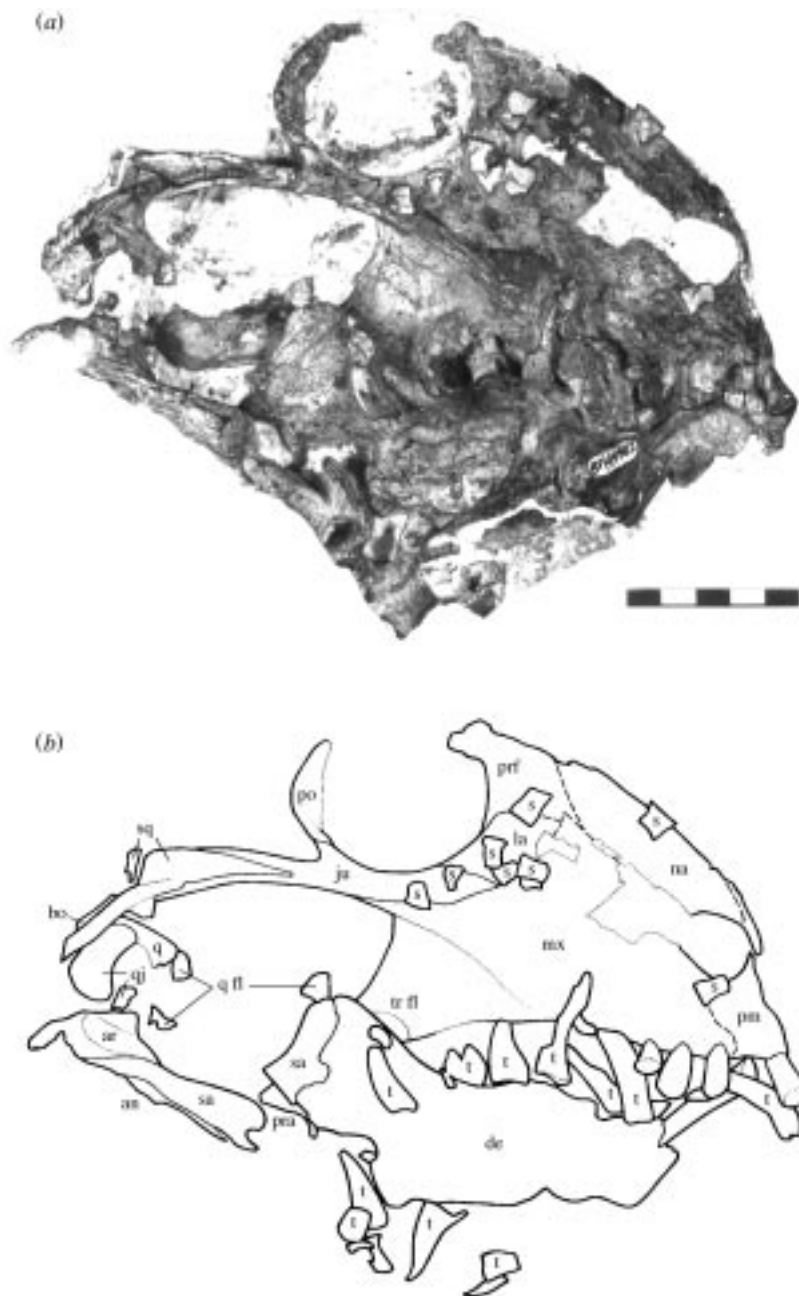


Figure 1. *Anomocephalus africanus* gen. et sp. nov. BP/1/5582: (a) photograph, and (b) interpretative drawing of the skull in right lateral view. Abbreviations: an, angular; ar, articular; bo, basioccipital; de, dentary; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; q, quadrate; qj, quadratojugal; q fl, quadrate flange of pterygoid; s, sclerotic ossicle; sa, surangular; sq, squamosal; t, disarticulated tooth; tr fl, transverse flange of pterygoid. Scale bar in centimetre blocks.

lamella of the quadrate remains of this bone. It is twice as broad as that of the quadratojugal. Posteriorly, the quadrate lamella lies pinched between the ventral process of the squamosal and the quadratojugal. The palate is represented by the lateral flange of the pterygoid and the transversum extending between it and the cheek; only small fragments remain of the quadrate flange of the pterygoid. The lateral process in outline resembles that illustrated for *Galeops* (Brinkman 1981). Laterally the process bears a triangular roughened surface, the torus transiliens. The bone between the torus and the cheek is smooth and the sutures for the ectopterygoid cannot be traced.

The mandible separated into two sections prior to fossilization, with the posterior fragment rotating 90° laterally from both the anterior fragment and the face of the skull. Its ventral region, including the reflected lamina, has been weathered away. The larger anterior fragment comprises the dentary and anterior parts of the surangular and the underlying prearticular; the splenial

is absent. As is typical for anomodonts, the dentary is deep dorsoventrally. Anteriorly, it bears conspicuously procumbent teeth which resemble those of the premaxilla. The dorsal margin rises posteriorly to contribute to a definite coronoid eminence. No depression that may indicate the lateral insertion of the adductor musculature is present below the level of the eminence. Ventral to the level of the coronoid eminence the dentary forms the anterior and dorsal margins of a mandibular fenestra. The surangular forms the posterior half of the coronoid eminence. Its lateral surface is slightly depressed with respect to that of the dentary, suggesting that the lateral adductor musculature may have inserted here, rather than further anteriorly as in venyukovioids, *Galeops* and dicynodonts (King 1994). The surangular tapers and curves posteroventrally to an attenuate tip appressed to the articular. The angular is marred heavily by surface damage and little can be said except that it appears to have had typical sutural relationships with neighbouring

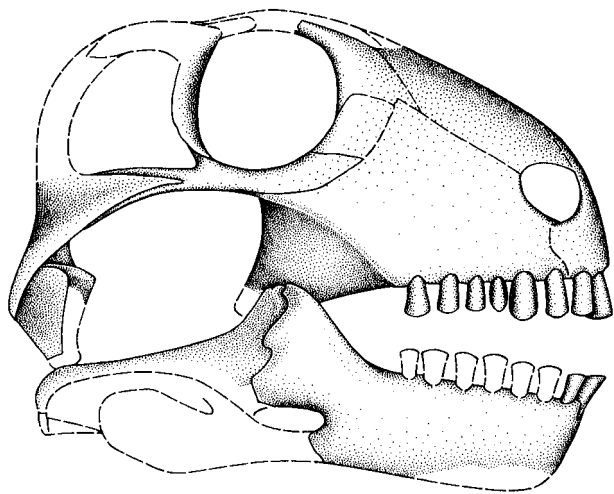


Figure 2. *Anomocephalus africanus* gen. et sp. nov. Reconstruction of the skull in right lateral view, two-fifths natural size. The outline of the quadrate flange of the pterygoid, known only from small, widely separated fragments, is omitted for clarity.

elements. The articular is visible in dorsal aspect and features two distinct articulating facets. They are twice as long anteroposteriorly as broad and are aligned roughly horizontally with faintly convex surfaces.

5. DISCUSSION

Figure 2 shows a restoration of the skull of *A. africanus* in right lateral view. The skull is remarkably deep and the peg-like marginal teeth are a rather conspicuous component of the feeding apparatus, unlike in most anomodonts (apart from canine tusks) except the venyukovioids. Together, these features are highly suggestive of a herbivorous diet. The reconstruction also suggests that the lateral flange of the pterygoid was horizontally aligned as in other basal anomodonts, rather than ventrolaterally directed, the plesiomorphic condition retained in gorgonopsians and therocephalians. In the latter therapsids the lateral flange actually projects well below the ventral margin of the skull. Several anomodont synapomorphies are well apparent in the skull reconstruction, namely the dorsally bowed zygomatic arch, the well-developed quadrate process of the squamosal and the presence of a mandibular fenestra.

A cladistic appraisal of anomodont phylogeny indicates that *Anomocephalus* is the most basal member of the group (figure 3). A phylogenetic position at the base of Anomodontia is relatively stable, requiring at least three steps beyond the most parsimonious resolution to move *Anomocephalus* deeper within Anomodontia. The synapomorphies for anomodont clades are given in the caption for figure 3. No postcranial characters are considered here, as most current knowledge about basal therapsids is derived from the skull. Apart from the inclusion of *Anomocephalus*, the interrelationships of the taxa shown in figure 3 do not differ from those in a recent analysis by Modesto & Rybczynski (1999). The basal phylogenetic position of *Anomocephalus* supports the recent postulate that anomodonts first evolved in African Gondwana. Optimization (Farris 1970; Maddison *et al.* 1984) of geographical distributions onto the tree

strongly suggests that the anomodonts diversified initially in Gondwana; whether this was from an anomodont ancestor that colonized African portions of Gondwana from Euramerica or from a more distant Gondwanan ancestor shared with therocephalians (and perhaps also gorgonopsians) cannot be determined with the available phylogenetic data. Concomitantly, venyukovioid anomodonts were derived from a single ancestor that dispersed into Euramerica from Gondwana.

In a recent review of terrestrial vertebrate biogeography of the Late Permian period, Modesto & Rybczynski (1999) concluded that several Kazanian amniote clades were characterized by marked endemism. Herbivorous groups, including anomodonts, were the most conspicuous clades showing such endemism. Their analysis of the interrelationships of the basal anomodonts, the first to include the most recently described member *Suminia getmanovi* (Ivakhnenko 1994; Rybczynski 1996), suggested that an African (Gondwanan) distribution was ancestral for Anomodontia. Their biostratigraphic conclusions contrasted with those of Rubidge & Hopson (1990), who suggested that anomodonts were dispersing freely between the northern and southern regions of Late Permian Pangea and those of earlier workers (e.g. Boonstra 1971; Sigogneau & Chudinov 1972) who postulated that therapsids, including the anomodonts, evolved first in Euramerica and then colonized Gondwana when climatic conditions became favourable (following the Permo-Carboniferous glaciation event: Kitching 1977). The latter 'classic' hypothesis was influenced by the presumed 'primitive' aspect of the Russian therapsids. However, equally 'primitive' forms have been recovered in recent years from the base of the Beaufort Group (Rubidge & Hopson 1990; Rubidge 1991, 1994).

The phylogenetic position of *Anomocephalus* provides compelling evidence (figure 3) that anomodonts initially diversified in Gondwana. It also supports the observation made by Modesto & Rybczynski (1999) that anomodonts were characterized by endemism early during their evolutionary history. Our findings contrast with those of other workers (Sues & Boy 1987; Milner 1993; Dilkes & Reisz 1996) who advocate a more homogeneous composition for Late Permian terrestrial vertebrate faunas. Milner (1993) used family-level groups in his review of Late Permian vertebrate biogeography and, thus, his study lacks the resolution of current phylogenetically based biogeographic analyses. In their study of Late Permian terrestrial vertebrate biogeography, Modesto & Rybczynski (1999) used more recent systematic and phylogenetic studies to identify endemism among several amniote groups during the Kazanian Stage and concluded that terrestrial vertebrate faunas became increasingly more homogeneous in the following Tatarian. Interestingly, the studies by Sues & Boy (1987) and Dilkes & Reisz (1996) concentrated on faunivorous taxa, whereas anomodonts are predominantly herbivores (King 1988), with the exception of *Patranomodon*, which was regarded as an omnivore by King (1994) and possibly the fossorial cistecephalid dicynodonts, which have been regarded as omnivores or faunivores by some authors (Cox 1972; King 1990) but as obligate herbivores by others (Keyser 1973; Zavada & Mentis 1992). It is possible that faunivory may have allowed taxa such as

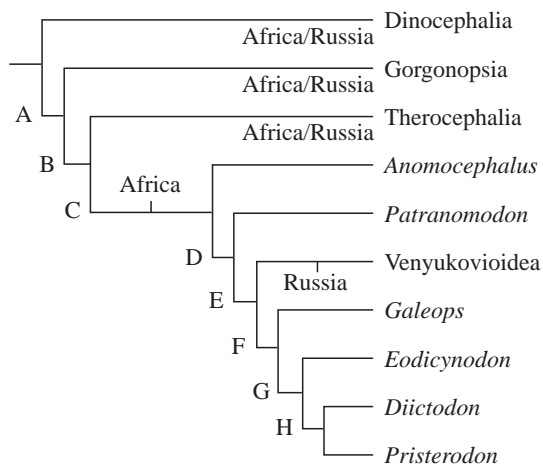


Figure 3. Cladogram illustrating basal anomodont interrelationships. This is the most parsimonious tree found by the branch-and-bound algorithm (delayed transformation) of PAUP 3.1, based on the 40 characters described in Appendix A and their distributions among the nine anomodont taxa and three outgroups listed in Appendix B. Tree length=66, consistency index (excluding uninformative characters)=0.761 and rescaled consistency index=0.684. Taxa with Gondwana distributions are in bold and distributions for other taxa are indicated on branches. As optimized onto this tree, the distribution of basal anomodonts indicates that a Gondwanan distribution is ancestral for anomodont therapsids (clade C), with a dispersal into Russian Euramerica by the venyukovoid ancestor (Venyukovioidea here includes *Otsheria*, *Ulemica* and *Suminia*, all Russian taxa). Abbreviations: Africa, Gondwanan distribution in what is now southern Africa; Russia, Euramerican distribution in what is now cis-Uralian Russia. Clades are diagnosed by the following synapomorphies, with numbers referring to characters described in Appendix A. Clade A: 18, 31, 35; clade B: 6*, 21, 25; clade C (Anomodontia): 1, 3, 13, 16, 35(2), 36; clade D: 6(2), 8*, 11, 12, 15*, 19(2)*, 24*, 26*, 27*; clade E: 14, 20, 22(2), 23, 30*, 38; clade F: 7, 10*, 27(2), 40*; clade G (Dicynodontia): -1, 2, 12(2), 13(2), 17, 22(3), 29, 33, 34*, 37, 39; clade H: 5, 28; Venyukovioidea: 3(2), 4, 9, -18, -19(1), 32, 34*. A minus sign indicates a reversal, asterisks denote characters that may apply at more inclusive nodes and derived states other than '1' are in parentheses (unless the apomorphy is a reversal).

procynosuchid cynodonts and varanopseid eupelycosaurs to enter a greater variety of terrestrial biotas more freely than contemporaneous plant eaters. Our work suggests that herbivory was acquired initially by anomodonts in Gondwana, perhaps in close association with the famous *Glossopteris* flora that characterized the Permian of the supercontinent. Similarly, Late Permian herbivores in Russian Euramerica may have co-evolved with the *Tatarina* peltasperma flora that characterized the Russian platform during this time (Meyen 1987). If anomodont lineages were co-evolving with elements of both floral complexes, it might account for the endemism observed for Kazanian herbivores. Taxonomic revision of the vast number of South African anomodont taxa, together with more detailed descriptions of anomodonts found elsewhere, are a necessary prerequisite for investigating how Tatarian terrestrial herbivores approached the biogeographic homogeneity observed for their faunivorous contemporaries.

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APPENDIX A: DESCRIPTION OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

1. Caniniform present and long (0), maxillary teeth decrease gradually in size posteriorly (1) or caniniform present but short (2).
2. Marginal teeth present anteriorly (0) or absent and instead an edentulous 'beak' formed by premaxilla, maxilla and dentary is present (1).
3. Fine serrations present (0), serrations absent (1) or coarse serrations present (2) on marginal teeth.
4. Denticulated cingulum absent (0) or present (1) on marginal teeth.
5. Premaxillae sutured (0) or fused (1) together.
6. Antorbital region long (0), short (1) or greatly abbreviated (2).
7. Antorbital median boss absent (0) or present and formed by paired nasals (1).
8. Septomaxilla posterodorsal spur present and separates widely nasal from maxilla (0) or absent and nasal-maxillary suture well developed (1).
9. Maxillary alveolar region short, occupies less than 53% of the ventral length of the bone (0) or tooth-bearing region long, occupying 72% or more of the ventral length of the bone (1).
10. Postorbital sharply tipped ventrally (0) or booted upon zygoma (1).
11. Zygomatic process of squamosal terminates posterior to postorbital bar (0) or contacts ventral process of postorbital anteriorly (1).
12. Zygomatic process of squamosal parasagittally deep (0), narrow and rod-like (1) or transversely expanded (2).
13. Base of subtemporal process of jugal parasagittally deep (0), narrow and rod-like (1) or transversely expanded (2).
14. Squamosal without (0) or with (1) lateral fossa for origin of lateral slip of adductor mandibulae externus muscle.
15. Squamosal posteroventral process absent (0) or present and extends ventrally to base of quadrate condyle (1).
16. Zygomatic arch roughly horizontal (0) or bowed dorsally (1).
17. Quadratojugal narrow and rod like (0) or plate-like (1) distally.
18. Pineal foramen raised on prominent boss (0) or opening flush with dorsal surface of skull roof (1).
19. Parietal bone absent and interparietal suture well developed anterior to pineal foramen (0), preparietal bone absent and interparietal suture anterior to pineal foramen greatly reduced by frontals (1) or preparietal bone present and interparietal suture reduced or absent anterior to pineal foramen (2).

20. Tabular separates squamosal from supraoccipital (0) or squamosal contacts supraoccipital (1).
21. Tabular contacts opisthotic (0) or separated from opisthotic by squamosal (1).
22. Internal narial shelf absent (0), narrow narial shelf formed by maxilla and palatine only (1), narrow narial shelf formed by premaxilla, maxilla and palatine (2) or narial shelf well developed and formed primarily by premaxilla and maxilla (3).
23. Premaxilla–Palatine contact absent (0) or present (1).
24. Ectopterygoid extends further posteriorly than palatine (0) or vice versa (1) in palatal aspect.
25. Palatine dentition present (0) or absent (1).
26. Pterygoid dentition present (0) or absent (1).
27. Lateral pterygoid process directed ventrolaterally (0), aligned horizontally (1) or directed ventrally (2).
28. Lateral pterygoid process wing-shaped (0) or reduced to small ridge (1).
29. Pterygoids contact anteriorly (0) or separated by vomers at interpterygoid vacuity (1).
30. Lateral palatal foramen absent (0) or present (1).
31. Epipterygoid separate from (0) or contacts (1) parietal.
32. Parasphenoid excluded from (0) or reaches (1) interpterygoid vacuity.
33. Dentaries sutured (0) or fused (1) at symphysis.
34. Lateral dentary shelf absent (0) or present (1).
35. Coronoid process or eminence absent (0), coronoid process formed solely by dentary present (1) or coronoid eminence present and formed by dentary and surangular (2).
36. Mandibular fenestra absent (0) or present (1).
37. Surangular vertical lamina present and lateral to articular (0) or absent (1).
38. Coronoid bone present (0) or absent (1).
39. Prearticular with (0) or without (1) lateral exposure posteriorly.
40. Jaw articulation permitting strictly orthal closure (0) or parasagittal movement (1).

APPENDIX B

Data matrix recording distribution of the cranial characters in nine anomodont taxa and three outgroups. Note that *Otsheria*, *Ulemica* and *Suminia* together comprise the Venyukovioidea as seen in figure 3. Gorgonopsia and *Ulemica* are polymorphic with respect to characters 6 and 33, respectively.

Dinocephalia	0000000000	0000000000	0000000000	0000000000
Gorgonopsia	0000000001	0000000120	0000000000	1000100000
	1			
Therocephalia	0000010000	0000000100	1100100000	1000100000
<i>Patranomodon</i>	1010020101	1110110120	1001?1100?	??00010000
<i>Otsheria</i>	10??020110	011011?01?	?2?111100?	?????1????
<i>Ulemica</i>	2021020110	0111110011	?21111100?	?1012101?0
				1
<i>Suminia</i>	1021020110	1111110011	1211111001	?101210101
<i>Galeops</i>	10??021101	111?110???	?21111200?	??00210101
<i>Eodicynodon</i>	0110021101	1221111121	1301112011	1011211111
<i>Pristerodon</i>	0120121100	1221111121	1311112111	1011211111
<i>Diictodon</i>	0110121101	1221111121	1311112111	1011211111
<i>Anomocephalus</i>	1010?10?00	0010011???	??????????	???021????

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